

Simple Model of Complex Reflection Behaviour in Two-Species Community

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Models of spatially distributed populations and/or communities are still a matter of challenge for the students working in population biology, ecology, environmental sciences and mathematical modelling. An adequate model pattern to describe, model and predict the impact of spatial structure on a community dynamics, as well as the migration processes themselves, is a key problem here. Adequate modelling of a spatial transfer of a being is the basic difficulty here. Currently, the basic methodology addressing

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the problem stands on implementation of partial differential equation of “reaction ÷ kinetics” type.

Such approach has serious discrepancy. To be valid, the models strongly require that the beings move over space randomly and spontaneously (aimlessly). This constraint is never met in nature; even microorganisms control their spatial redistribution [1–3].

Previously, there was proposed an approached to model a dynamics of a community with respect to spatial effects based on the (micro)evolutionary principle [3–5]. In brief, the principle forces beings to migrate in the manner improving their existence. An improvement of existence of beings is here the key question; the answer is given by the net reproduction function [5–8] $k(\rho, \vec{r})$. Here $\rho = \rho(\vec{r})$ is the (local) density of a population, and \vec{r} is the point in space. Obviously, the population density ρ depends on the point at space.

Net reproduction function results from two effects: the former is reproduction, and the latter is inheritance [6–8]. If these two effects take place, then an equation of a dynamics of biological entity must look like

$$\dot{\rho}(\vec{r}, t) = \rho(\vec{r}, t) \cdot k(\rho(\vec{r}, t)) \quad \text{or} \quad \rho_{t+1}(\vec{r}, t) = \rho_t(\vec{r}, t) \cdot k(\rho_t(\vec{r}, t)) , \quad (1)$$

for discrete time. Here $k(\rho)$ ($k(N)$, respectively) is the net reproduction function. It must be bounded above. The equations (1) are the equations with inheritance. A comprehensive theory of such equations, in the most general case, including the investigation of three types of evolutionary stability see in [5–8]. The most general result is that net reproduction function $k(\rho)$ must meet the extreme principle, for any free evolving biological community. $k(\rho)$ is maximal for those species (entities) that sustained during the evolution; $k(\rho) = 0$ in continuous time case, and $k(\rho) = 1$ for discrete time.

Finally, the basic issue of our model of spatially dependent dynamics of a community is that any migration must not be a random walk, but result in a growth of net reproduction. Further, we shall consider a model in discrete time and discrete space sites (called stations). A study of continuous model brings severe technical problems, so we shall start from a discrete case.

1 Model of Two-Species Community

We shall study a dynamics of a community consisting of two species; they are supposed to be “*prey ÷ predator*” related. It means, that one species exists due to external resources, but other one lives due to the beings of the former species. It is also supposed, that both species occupy two stations¹ and migration means a transfer of being (of any species) from station to station. Any other movements (inevitable in real situation) are neglected and supposed to have no effect on a community dynamics.

The dynamics of (isolated) subcommunity occupying a station is supposed to follow the discrete analogue of classic Lotka-Volterra equation, if no migration takes place:

$$\begin{aligned} N_{t+1} &= N_t \cdot (a - bN_t - fX_t) & M_{t+1} &= M_t \cdot (c - dM_t - gY_t) \\ X_{t+1} &= X_t \cdot (\varepsilon fN_t - hX_t) & Y_{t+1} &= Y_t \cdot (\varepsilon gM_t - kY_t) . \end{aligned} \quad (2)$$

Here N_t, X_t are the abundances of prey and predator, respectively, at the first station, and M_t, Y_t are similar variables at the second station. Parameters a and c determine a fertility of prey population, in the relevant stations; parameters b and d describe the density-dependent self-regulation of this population, in relevant station. Parameters h and k describe similar

¹These are the sites considered together with the environmental conditions.

density-dependent regulation at predator subpopulations. Parameters f and g describe, in general form, an efficiency of the interaction of the beings of these two species, including a success of hunting, success of escape, etc., in corresponding stations. Finally, ε represents an efficiency of the conversion of prey biomass into the predator biomass.

1.1 Basic Model of Migration

Parameter p , $0 \leq p \leq 1$ is a mobility of prey beings; similar, q , $0 \leq q \leq 1$ is mobility of predator beings. These parameters are the transfer cost and might be interpreted as a probability of the successful migration from one station to other; success here means that no damage for further reproduction had taken place. Migration from station **A** to station **B** starts, if living conditions “there” are better, than “here”, with respect to the transfer cost:

$$\begin{aligned} (a - bN_t - fX_t) &< p \cdot (c - dM_t - gY_t) , \\ (\varepsilon fN_t - hX_t) &< q \cdot (\varepsilon gM_t - kY_t) , \end{aligned} \tag{3}$$

for prey and predator beings, respectively. It should be stressed, that the migration act is executed independently by each being, while the model considers it as a population event. The backward migration conditions are defined similarly:

$$\begin{aligned} p \cdot (a - bN_t - fX_t) &> (c - dM_t - gY_t) , \\ q \cdot (\varepsilon fN_t - hX_t) &> (\varepsilon gM_t - kY_t) . \end{aligned} \tag{4}$$

Migration act runs each time moment t , for both species independently. If neither of the inequalities (3, 4) are fulfilled, then no migration takes place, at the given time moment t . Prey migration flux Δ (predator migration flux

Θ , respectively) must equalize inequalities (3, 4):

$$\begin{aligned} (a - b(N_t - \Delta) - fX_t) &= p \cdot (c - d(M_t + p\Delta) - gY_t) , \\ (\varepsilon fN_t - h(X_t - \Theta)) &= q \cdot (\varepsilon gM_t - k(Y_t + q\Theta)) \end{aligned} \quad (5a)$$

for the case (3), or

$$\begin{aligned} p \cdot (a - b(N_t + p\Delta) - fX_t) &= (c - d(M_t - \Delta) - gY_t) , \\ q \cdot (\varepsilon fN_t - h(X_t + q\Theta)) &= (\varepsilon gM_t - k(Y_t - \Theta)) \end{aligned} \quad (5b)$$

for the case (4). Then, Δ (Θ , respectively) is equal to

$$\Delta = \frac{pc - a + bN - pdM + fX - pgY}{b + p^2d}, \quad \Theta = \frac{hX + \varepsilon qgM - \varepsilon fN - qkY}{h + q^2k} \quad (6a)$$

for migration form station **A** to station **B**, and

$$\Delta = \frac{pa - c + dM - pbN + gY - pfX}{d + p^2b}, \quad \Theta = \frac{kY + \varepsilon qfN - \varepsilon gM - qhX}{k + q^2h} \quad (6b)$$

for the backward migration.

Finally, let's outline how the basic model (2 – 6) works. For each time moment t , a direction and the migration fluxes (Δ and Θ , respectively) are determined. Then, the species redistribute themselves according to the Eqs. (6). Then, the abundances of the next generation $\{N_{t+1}, X_{t+1}; M_{t+1}, Y_{t+1}\}$ are determined, according to (2), with the relevant abundances of the current generation $\{\tilde{N}_t, \tilde{X}_t; \tilde{M}_t, \tilde{Y}_t\}$ defined by (5). If no migration must take place at the current timer moment t , the the stage with species redistribution is omitted.

1.2 Reflexive Behaviour

Reflection in behaviour means an ability of a being to foresee and/or predict the behaviour of an opponent, in a competitive behavioural act. An implementation of reflexive behavioural strategy by animals is a well known. Not

discussing here psychological or ethological aspects of such strategies implementation, let concentrate on a simple model revealing the dynamic effects of them.

Basic model (2 – 6) does not exhibit any reflexive behaviour. An introduction of that latter into the basic model may only be concerned with the spatial redistribution. In other words, reflection of the optimal migration behaviour means that a being is able to “foresee” the migration behaviour of a competitive species being. With respect to it, one may assume the following patterns of the reflection in the behaviour of the species: (i) preys reflect predators; (ii) predators reflect preys, and, finally, (iii) both species reflect each other.

Thus, within the framework of our model, a reflection means that the species manifesting a reflection in the behaviour, detects the migration conditions and chooses the migration flux according to the abundances of a competing species, that would be produced due to the migration of that latter, not the current ones. In case (i) formula for Θ would remain the same, but the formula for Δ would change for

$$\Delta = \begin{cases} \frac{pc - a + bN - pdM + f\tilde{X} - pg\tilde{Y}}{b + p^2d} & \text{or} \\ \frac{pa - c + dM - pbN + g\tilde{Y} - pf\tilde{X}}{d + p^2b}, \end{cases} \quad (7)$$

in dependence of the migration direction. Here \tilde{X} and \tilde{Y} are determined according to (5).

Reciprocally, \tilde{N} and \tilde{M} are determined according to (5), for the case (ii),

but migration flux Θ of predator would be determined by

$$\Theta = \begin{cases} \frac{hX + \varepsilon q g \widetilde{M} - \varepsilon f \widetilde{N} - qkY}{h + q^2k} & \text{or} \\ \frac{kY + \varepsilon q f \widetilde{N} - \varepsilon g \widetilde{M} - qhX}{k + q^2h}, \end{cases} \quad (8)$$

in dependance of the migration direction.

Finally, if both species reciprocally reflect the behaviour of each other, then basic model should be changed for the following one. On the first stage, both species determine the migration fluxes according to basic model (5, 6). Then, they redefine the migration fluxes (and migration direction, as well as the fact of migration) so, that each species changes the current abundances of the competitive beings for those that could be produced due to a migration rule determined by the basic model. So, they redefine the fluxes, redistribute themselves between the stations, and reproduce.

2 Results and Discussion

Main purpose of this paper is to figure out the sets of the parameters providing an evolutionary advantage to a bearer of some (reflexive, or not) spatial distribution strategy. Evolutionary advantage here is understood as an excess of the total abundance of some species realizing reflexive strategy, in comparison to the same species in case of realization of regular (non-reflexive) strategy.

Table 1 shows the result of simulation observed for the following parameters sets:

$$\#1 \quad a = 3.1, \quad c = 1.49999, \quad b = 0.00098, \quad d = 0.00099, \quad h = 0.00052, \quad k = 0.0005, \quad f = g = 0.00542, \quad \varepsilon = 0.099, \quad p = q = 0.99.$$

#2 $a = 2.5, c = 1.49999, b = 0.00098, d = 0.00099, h = k = 0.0005,$
 $f = g = 0.0054, \varepsilon = 0.099, p = q = 0.99.$

#3 $a = c = 1.5, b = d = 0.0001, h = 0.0001, k = 0.0005, f = g = 0.0059,$
 $\varepsilon = 0.05, p = q = 0.99.$

#4 $a = c = 1.5, b = d = 0.0001, h = k = 0.00001, f = 0.0059, g = 0.0049,$
 $\varepsilon = 0.05, p = q = 0.99.$

#5 $a = 1.7, c = 1.5, b = d = 0.0001, h = k = 0.00001, f = g = 0.005,$
 $\varepsilon = 0.05, p = q = 0.99.$

#6 $a = 2.2, c = 2.1, b = d = 0.0001, h = k = 0.00001, f = g = 0.005,$
 $\varepsilon = 0.05, p = q = 0.99.$

First of all, it should be said, that the basic model (2 – 6) exhibits a great diversity of limit regimes. It may be a steady state (in both stations, for both species), limit cycles of various length, and a complex irregular behaviour looking like a dynamic chaos. All these peculiar regimes may be met in combinations, with respect to a station and/of a species. In general, a decrease of transfer cost p and q yields a simplification of an observed regime. Both the basic model (2 – 6) and its versions implementing various reflexive strategies of spatial distribution yield an expansion of the area of permissible parameter values, and the area of the phase space (i.e., abundance figures). All these issues are very interesting, from the point of view of the study of the models of optimally migrating communities, but they fall beyond the scope of our research.

What we do, was a comparative study of those four models (basic model and three versions with reflexive behaviour) from the point of view of the evolutionary advantage. In fact, we tried various combinations of the parameters, similar for all four models, in order to identify the model that

Table 1: Comparison of various strategies of space distribution. S — type of strategy: 1 – basic model, 2 – model i , 3 – model ii , 4 – model iii .

S	N	X	M	Y	S	N	X	M	Y
Set of parameter # 1					Set of parameter # 2				
1	2089	5	4539	6	1	1513.5	1.4	1952.5	56.2
2	1930	20.5	2368	50	2	1438.8	4.1	2244.6	55.6
3	1692.9	43.7	1849.9	41.7	3	1524.5	0.47	1938.6	56.7
4	2142	0.1	5040	0.1	4	1530	0.01	5047	0.01
Set of parameter # 3					Set of parameter # 4				
1	3697	18	3698	18	1	3542	20.9	4073	14.3
2	4999	0.01	4999	0.01	2	4997	0.01	4998	0.01
3	3873	6.4	3869	6.5	3	3619	11.2	3739	8
4	4189	13.8	4190	13.8	4	4325	12.5	4384	11.5
Set of parameter # 5					Set of parameter # 6				
1	6994	0.05	4996	0.01	1	5.4	0.1	4.4	0.04
2	5688	32.1	4122	11.6	2	8406	80.5	7172	69.3
3	4664	19.5	2961	13.9	3	3.6	0.07	3.6	0.1
4	5412	30.5	4086	18.7	4	8404	80.5	7171	69.3

yields the highest total abundance of the species.

To answer this question, we have carried out a series of simulations (computational experiments). We calculated the abundance of each species, in each station, for four models with the same parameter set. Then, the abundances of prey subpopulation (of predator subpopulation, in turn) were added. Table 1 shows the results of such comparison. The parameters yield-

ing the observed regimes are shown below the Table.

It is evident, that there exist the parameters sets yielding an evolutionary advantage for various types of space distribution strategies. Yet, we did not studied carefully the peculiarities of the limit regimes relevant to each evolutionary advantageous situation, meanwhile, one may expect that the reflexive strategies provide an advantage for rather regular limit regimes, while the non-reflexive strategy of space distribution is advantageous for chaotic-like, complicated limit regimes.

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